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Inheritance of rest period of seeds and certain other characters in Arachis hypogaea, L, peanut

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INHERITANCE OF REST PERIOD OF SEEDS AND CERTAIN OTHER CHARACTERS IN ARACHIS HYPOGAEA, L., PEANUT

by

Fred H. Hull

A Thesis Submitted to the Graduate Faculty
for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject Genetics

Approved:

Signature was redacted for privacy.

In charge of Major Work

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Dean of Graduate College

Iowa State College
1934

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INTRODUCTION

Genetic studies of the required rest period of seeds, seed shape, seed coat color, yellow seedlings, Valencia plant type and brachytic, dwarf plants in the common peanut are reported in this paper. Biometric tests for associations of the first five of these characters among themselves and with 17 others are also presented. The above named characters with the exception of rest period of seeds were the only ones of 23 which gave evident Mendelian ratios in a number of crosses of different varieties of cultivated peanuts.

These varieties are all American types which fall naturally into three groups: runner, Spanish and Valencia. This classification is not entirely in agreement with the earlier system of Chevalier (1933) or Hayes (1933), but is the only grouping which seemed satisfactory for the present purpose.

The runner group includes the Virginia and common runner varieties, which are definitely prostrate except Virginia Bunch which is semi-erect. This group has dark green foliage, occasionally three seeds in a nut, long seeds, russet seed coat, and its seeds require a rest period of at least several weeks after maturity before germinating under average field conditions. The Spanish group, known sometimes as Little White

Spanish, consists of erect types, with light green foliage, very rarely if ever more than two seeds in a nut, short seeds, tan seed coat, and most of the seeds require no rest period at all. The Valencia group includes the varieties Tennessee Red, Tennessee White, and Porte Alegre. This group is characterized by many three- and four-seeded nuts and by a very sparse branching habit. The varieties named are all erect but Chevalier (1933) describes two African forms which possess the distinguishing characters and are fully prostrate. The foliage is dark green, seeds short or long, seed coat purple, red, russet or tan, and most seeds require no rest period. This classification of the varieties of Arachis hypogaea is further supported by the genetic evidence of duplicate genes to be discussed later.

Two other species of peanuts, Arachis Nambyquarae and A. Rasteiro are cultivated to a limited extent in Brazil and a selected strain of each was included in the present studies. Chevalier (1933) states that these two species are merely distinct races of A. hypogaea.

This view of Chevalier has not been contradicted by cytological evidence as reviewed and reported by Husted (1933). There seems to be little doubt that the three cultivated species of peanuts have typically 40 diploid or 20 haploid chromosomes. Husted's report of secondary pairing and of

irregularities in meiosis with the occurrence of univalents, trivalents, quadrivalents, and rings of as many as six indicates polyploidy, probably tetraploidy. Tetraploidy is also indicated by several pairs of duplicate genes, reported by Hayes (1933) and in the present paper. The probable occurrence of 20-chromosome types among the wild species of South America is thus suggested. If irregular associations at meiosis are frequent unusual ratios will be found with some characters. The statement of Badami (1928), that some characters give simple ratios in certain crosses and complex series in others, is suggestive.

Previous Inheritance Studies with Peanuts

These may be summarized as follows:

1. Red seed dominant to russet or tan (3:1), Van der Stok (1910), Badami (1928), Stokes and Hull (1930), Hayes (1933).

2. Prostrate habit dominant to erect, Badami two factors, Hayes (15:1).

3. Chlorophyll; three factors with triple dominant dark green and triple recessive albino, Badami.

4. Dark red stem dominant to light red (3:1), Hayes; violet tinge dominant, appears to be associated with hardiness, Badami.

5. Long seed dominant to short (15:1), Hayes.

6. Fertile dominant to sterile, complementary[1] (15:1), Hayes.

7. Normal leaf dominant to crinkled leaf, complementary[1] (15:1), Hayes.

8. Leaf rachis presence dominant to absence, complementary[1] (15:1) Hayes.

9. No constriction on nuts double dominant, two factors, Badami.

10. Leaflet size intermediate in F_1 and wide range in F_2, Badami.

11. Large nut dominant to small, three factors, Badami.

12. Pericarp thickness, five factors; thin pericarp linked with pygmy seed, Badami.

13. Deep reticulations on pericarp dominant to shallow, at least four factors, Badami.

14. Hairy stem dominant to less hairy, Badami.

15. Three- or many-seeded pods dominant to less than three-seeded, at least three factors, Badami.

16. Long growing season dominant to short, Badami.

17. Early fading flowers dominant to late, Hayes.

18. Deeply colored corolla dominant to light, Hayes.

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[1]Hayes (1933), evidently uses the term complementary to describe the interaction of two pairs of genes which are ordinarily termed duplicates.

19. Red color on leaflet vein dominant to its absence, Hayes.

20. Sine leaf shape dominant to Valencia shape, Hayes.

21. Required rest period of seeds partially dominant to its absence, Stokes and Hull.

22. Variegated seed due to rupture of seed coat as found in A. Nambyquarae partially dominant to its absence in A. hypogaea, Stokes and Hull.

Badami found drought resistance associated with dark green leaf. Hayes states, "No characters that exhibit clean-cut segregation show any connection with one another." He reports that eight characters: length of leaves, length of petiole, length of rachis (leaf), length of sheath, width of leaves, corolla color, hairs on petiole, and number of seeds, all showed marked correlations with each other.

GENERAL METHODS AND MATERIALS

Natural cross pollination is generally conceded to be rare in peanuts. No plants of hybrid appearance have been found among pure strains of diverse type grown together at the Florida station for a number of years. Now strains originated by selection of single plants have been uniform and constant.

A group of pure strains was obtained by isolating single plants from each of the distinct American varieties or types of cultivated peanuts. Hybrids were secured by hand pollination and grown in field cultures with the parent strains. Records were made of 23 characters in the different lots. If no definite classification of a character was possible numerical grades were used. The experiments were designed primarily for a study of the inheritance of the required rest period of seeds which was sometimes detrimental to the study of other characters. Rest period is of first importance in peanut improvement work in Florida, for which purpose this experiment was conducted.

Pedigree numbers of the selected strains of peanuts and the stock from which they originated are listed below.

No. 1, from an improved strain of Spanish Peanuts furnished by Mr. J. H. Beattie of the U. S. D. A.

No. 3, from a selected strain of Spanish originated at the Florida station by a single plant selection in 1921.

No. 4, from Tennessee Red.

No. 6, from Tennessee White.

No. 7, from Valencia.

No. 8, from Florida Runner.

No. 9, from Virginia Runner.

No. 11, from Virginia Bunch.

No. 12, from Spanish.

No. 13, from Spanish, variety Macspan from the Texas Experiment Station.

No. 14, from Jumbo Runner.

No. 15, from the subspecies, Nambyquarae.

No. 21, from the subspecies, Rasteiro.

No. 221, from Dixie Giant, an unusually large-seeded strain of Jumbo Runner type selected by Mr. J. H. Beattie of the U. S. D. A.

REQUIRED REST PERIOD OF SEEDS

It has been shown by Stokes and Hull (1930) that peanut seeds which require a rest period will imbibe large amounts of water if placed in moist sand, and may remain in that condition many months before germinating. Embryos of such peanuts give no external indication of change after the seeds are mature and before germination begins. Presumably chemical or physical changes occur internally to bring the rest period to an end. The term "after-ripening" has been used by physiologists to refer collectively to such changes (Miller, 1931), and is so used in this paper.

Stokes and Hull also reported that peanuts of the Spanish and Valencia groups required little or no rest period while those of the runner group required a rest period of several weeks or more. Hybrid seeds produced by applying the pollen of runner plants to the stigmas of Spanish plants required rest periods intermediate in duration to those of selfed seeds from the parents. This indicates that rest period is controlled to a large extent by the genotype of the embryo itself and not entirely, if at all, by that of maternal tissue.

The situation in small grains, as reported by Deming and Robertson (1933), must be quite similar. They found marked

differences among common strains of wheat, oats, and barley in ability of the seeds to germinate within 10 days after harvest. An F_1 hybrid of Marquis and Federation wheats was more like the dormant Marquis parent, indicating some degree of dominance.

Inheritance of premature germination in maize has been extensively studied by several workers, notably Mangelsdorf (1930). At least 15 recessive genes were found to affect premature germination. Some of the genes were complementary in action while others behaved as duplicates, triplicates, or quadruplicates. Delayed germination after maturity is apparently unknown in maize while premature germination has not been definitely identified in peanuts but is suspected of occurring occasionally.

The inheritance of required rest period of peanut seeds was studied further with selected strains of the several groups and hybrids between them. Rest periods were measured by harvesting individual plants when a characteristic stage of maturity was reached and planting the shelled seeds 10 days later in a greenhouse. Considerable variation in the stage of maturity of nuts on a single plant usually existed. Those used for the tests of rest period were selected within a narrow range judged by the color developed on the inner surface of the hull. By selecting the older seeds of plants slightly immature and the younger seeds of those fully mature it was possible to secure samples well balanced in that respect.

The seeds were planted in boxes of clean sand to a depth of one-half inch and left undisturbed until they emerged as seedlings. Conditions under which seeds requiring no further rest would emerge in 6 to 12 days were maintained continuously. The temperature of the sand was measured with a self-recording instrument and found to range from 10°C. to 35°C. However, these extremes were not often reached. Differences in mean monthly temperatures throughout the entire year were not greater than 6°C. Moisture control was effected by saturating the sand thoroughly whenever it was dry on the surface. Under these conditions germination was usually satisfactory and was equally high in more dormant and less dormant families as shown in Table V.

Since it was impossible to control temperature and moisture closely, experiments to test their effects on the rate of after-ripening were conducted. These tests also provided information on the general shape of the after-ripening curve which has been useful in interpreting genetic data.

Seeds of the Florida Runner variety which have a long rest requirement were placed in storage after harvest in cold rooms at -15°C., 0°C., 3°C., and 5°C., in an open shed at 20-25°C., and in incubators at 30°C., 40°C., and 50°C.[1] Three other samples were stored in the shed in dessicator chambers

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[1]By courtesy of the Departments of Horticulture and Plant Pathology, Florida Experiment Station.

over water, over a drying agent, and with no reagent and the lid slightly lifted. A third test was made with seeds of Spanish strain[1] No. 1, which had the least rest requirement of any available, to learn if the need of a rest period in such seeds would reappear or increase at lower temperatures. One lot was held in the shed continuously after harvest, a second was held in the shed 48 hours and then at 3°C., and a third was held in the shed 10 days and then at 3°C. Sub-samples of 10 seeds were taken from each lot of every test at weekly intervals, or more often when necessary, and planted in the greenhouse to determine the rest requirement still remaining.

Principal results of temperature tests are pictured in Figures 1 and 2. The curves in those figures were drawn freehand through the plotted points with a broad application of the principle of fitting by least squares. It may be seen in Figure 1 that after-ripening progressed rapidly at higher temperatures and much more slowly at lower temperatures. Also the curves of shed storage and 40°C. cut abruptly into the base line or threshold of germination indicating no reaction end-point at that level. The same effect was observed in six other curves not presented here. An apparent asymptotic approach of one low temperature curve in Figure 1 to the base line is thought to be not real since periodicity with minima

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[1]Origins of pure strains given on page 9.

and maxima at different levels was observed in all low temperature curves of Florida Runner seeds.

Rest period quickly disappeared with Spanish seeds stored in the shed continuously as shown in the lower curve of Figure 2. The center curve shows that transfer from the shed to 3°C. at about the time rest requirement disappeared caused a rapid increase of rest period for a few days followed by a slow decline. In the upper curve it appears that transfer to 3°C. eight days later did not result in a measurable rest period until after about 10 days of cold storage. Presumably the after-ripening process had progressed some distance below the threshold of germination in eight days and the succeeding 10 days of cold storage were occupied in reversing and returning it to that level.

Moisture contents of the three lots of Florida Runner seeds in dessicator chambers were 7 per cent, 9 per cent, and 16 per cent at 45 days after harvest when most of them were through the rest period. No consistent differences in rates of after-ripening were found.

It is concluded from the several temperature and moisture tests that those factors were controlled sufficiently to provide reasonable accuracy in rest period determinations. There is no evidence of sudden changes in temperature being effective in breaking or inducing dormancy. This is particularly gratifying since such changes were sometimes unavoidable in the greenhouse.

The slope of the shed storage curve in Figure 1 is a measure of the relative rates of after-ripening in seeds stored in the shed and planted in the greenhouse. That curve has a slope of about four and one-half. The mean slope of it and two other shed storage curves is about two. All of these curves are essentially straight lines so it is concluded that the practice of delaying planting 10 days after maturity has cut off about 20 days from the left end of the range of rest period in inheritance studies. Unfortunately, delayed planting was necessary because the seeds could not be hulled without injury before they were partially cured. Hulling was necessary to obtain accurate counts and to estimate maturity and because there were great differences in thickness and texture of the hulls in different strains.

Data on the rest periods of pure strains of peanuts and their hybrids are summarized in Tables I to VII. Table I includes the less dormant strains of the Spanish and Valencia groups while Table II includes the more dormant strains of the runner group and A. Nambyquarae and A. Rasteiro. Table III includes one F_1 and three F_2 hybrids with the data on their parents repeated for convenience. Most of the rest period tests were made with four crosses between Spanish and runner peanuts on F_3 seeds of three of them and both F_3 and F_4 of the fourth. The data on this latter cross are summarized in Table IV and the F_4 distributions of a sample of its F_2 families are given

in Table V. Mean rest periods of all of the hybrids tested and their parents are summarized in Table VII.

The tables include frequency distributions of both single seeds and plant means in terms of days from planting to emergence. Means, variances, standard errors of the means, numbers tested, and germination percentages are also given. Frequencies are expressed by percentage in each class for ease of comparison.

A spurt of early emergence occurred in all but the most dormant lots, usually on the eighth day after planting but varying from the sixth to the twelfth with different strains and with slight variations in environment. This first spurt was thought to mark the point of zero days rest period but since it was not definite in the more dormant lots no general conversion of the data into terms of rest period was made. The upper limit of first classes of the frequency distributions was set at 17 days after planting to include the few weak stragglers which really belonged to the first class. Daily emergence was very low in the first two or three weeks succeeding the first spurt so it is really unimportant whether the upper limit of the first class be set at 13 or 25 days after planting. It must be understood, however, that frequencies of first classes of single seed distributions consist almost wholly of seeds with no rest requirement at planting time. If accurate conversions of the data into terms of rest period

could be made, the modes and almost the entire frequencies of first classes would be found at zero.

This fact is to be remembered in searching for causes of the very marked skewness of most of the frequency distributions. The search must be directed first to the distributions of single seeds since those of plant means may have been complicated by the process of averaging. The general situation can be observed to the best advantage in Tables I, II, and V where different strains and hybrid families are arrayed in order of mean number of days to emergence. There is no apparent difference in the distributions of pure strains and hybrid families except greater dispersion of the latter which is no doubt due to genetic variance. The less dormant families have highly skewed distributions with very pronounced modes at zero days rest. Proceeding to more dormant types, the modes become less pronounced and finally move away from zero. Still lower in the tables, distributions are found with two modes one of which is at zero. Finally the most dormant families have only one mode near the center of a nearly symmetrical distribution. There are some exceptions to this picture but the general scheme is clear enough.

An apparently false mode is found at zero days rest regardless of the position of the sample on the range with two exceptions. Where the true mode is located just above zero it overshadows the false mode at zero. Where the range of the

sample is far to the right no false mode at zero is apparent and the distribution is generally symmetrical. It is to be recalled that about 20 days of the left end of the range were cut off by delaying planting to 10 days after maturity. This addition could hardly be expected to change the general picture very much. Nor does it seem reasonable to suppose that a different environment, e.g. storage at low temperature for a few days between maturity and planting, would have eliminated skewness. The data suggest multiple gene inheritance with the genetic range or range of genotype extending well to the left of the zero point of the physical character.

It is not impossible that the condition built up in seeds by the so-called after-ripening process may already exist in some seeds at maturity in degrees well above the requirement for germination. It has been shown that the process very probably continues beyond the germination threshold after maturity in seeds having some initial rest requirement. Inheritance of this condition by the familiar quantitative scheme would appear possible so it is probably unnecessary to suppose any special type of gene interaction but only that the lower physical limit of rest period is found well up on the genetic range.

Returning to distributions of plant means, it is more than likely that the location of their modes slightly above those of the distributions of single seeds is due to nearly

every plant having at least a few seeds requiring some rest period. Since none can have negative rest periods the plant means are almost always somewhat greater than zero days rest.

Frequency distributions of seven other quantitative characters in the same cultures were found to be generally symmetrical with one exception. Distributions of seed-cells (ovules) per plant are markedly skewed to the left but much less so than those of rest period. It is not unlikely that the principal cause of skewness is, as suggested with rest period, extension of the genetic range below the zero point of the physical character. Hayes (1933) presents six distributions from the F_3 generation of one cross, four of which appear symmetrical. The distribution of number of seeds is very similar to that of number of seed-cells noted above in the present study. Hayes classed number of hairs on petiole in six grades by observation and derived a distribution slightly skewed to the right but actual counts might have produced symmetry.

Since experimental errors were large in rest period tests and standard errors of skewed distributions must be rejected, it is desirable to consider an estimate of genetic variance in hybrid families before comparing mean values. No comprehensive calculations were possible but an estimate was obtained from the two F_3 families whose F_4 distributions are shown at the bottom of Table V. Neither distribution is badly distorted. Analyses of the F_4 variances into between and within F_3

families are shown in Table VI. In both cases the mean squares between F_3 families are highly significant. Since the two families lie towards one extreme of the range where less genetic variance is expected and since a marked decrease in genetic variance is expected with each generation of self-fertilization, a significant proportion of genetic variance must have occurred generally throughout the F_2 and F_3 hybrid populations.

Comparisons of the less dormant pure strains in Table I by standard errors of differences cannot be made because of skewness of their distributions. However, the two tests on strain No. 7 span most of the table so that the existence of more than three genetic types is not demonstrable from the data. The more dormant strains are compared by standard errors of differences in Table II (b). Since strain No. 11 is significantly different from both strains 21 and 8 which are at opposite ends of the range, it is probable that three genetically distinct types, if not more, are present. Further information on the pure strains of both groups appears in their breeding behavior as shown in Table VII where comparisons of two strains of one group in crosses with a single strain of the other group are possible. The comparisons are (21, 14 x 7)[1], (7, 3 x 21), (7, 1 x 14), (7, 13 x 14), (1, 13 x 14),

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[1]Origins of pure strains used as parents are given on page 9.

(14, 8 x 13) and (3, 13 x 8). In five of these seven comparisons the hybrid means and means of the non-recurrent parents lie in the order expected by the usual theory of quantitative inheritance which order is unchanged by the qualification of a large portion of the genetic range being hidden. The two exceptions involve F_2 tests with small numbers of seeds. Five of the comparisons are between strains of the less dormant group with four of them in the expected order indicating probable genetic differences in that group.

Relative positions of the means of parent strains, F_1, and later generation hybrids may be studied in Table VII. It is first necessary, however, to recognize distortions arising from an excess of experimental errors near zero and from delay of planting in rest period tests until 10 days after maturity. Experimental errors, arising from accidental variations in development of seeds and in their environment during rest period tests, were large. Negative errors could not extend below zero days rest while positive errors were not restricted. These errors cannot be calculated but it may be noted that parent strains were uniform in other respects and apparently very nearly homozygous. Also, more than 50 per cent of the frequency of each less dormant parent is concentrated in a narrow interval centering on about eight days after planting. It is concluded that the true positions of less dormant parents are not above that point or that their positions on the genetic

range are not above the point of zero days rest period with the present scale of measurement. Parenthetically, it may be stated that unequal limitation of positive and negative experimental errors appears to explain adequately skewness in the distributions of less dormant pure strains.

Rest period tests were planted 10 days after maturity, and it has been established that the time from planting to emergence was about 20 days less than if plantings had been made immediately. However, seeds having less than 20 days rest requirement at maturity could not have their time to emergence shortened by more than the length of the initial rest requirement, and those having no rest requirement at maturity would, in either planting, have usually required eight days to emerge. Errors in more dormant parent strains and probably in the F_1 may be corrected by adding 20 days to the means. Samples having no initial rest requirement need no correction while intermediate samples need an indeterminate correction of something less than 20 days.

The F_1 comparison is further handicapped by failure to obtain a test on the more dormant parent because of constantly poor quality of its seeds. For example, strain No. 14, from the same variety, has a mean of 154 days and the range of the more dormant group is 112 to 210. The mean of the less dormant parent can hardly be greater than eight days if correction for unequal experimental errors is made. The sample of 10 F_1 seeds

has a mean of 110 days. All of these values are subject to correction for delay in planting. The correction is 20 days for the greater parent and F_1 and probably somewhat less for the lesser parent. However, if the maximum correction is made on the lesser parent, the parental mid-point may be expected in the range of 80 to 129 days, probably near 101. If the lesser parent is a minimum type with no rest requirement after maturity and needing no correction, 10 days should be subtracted from these parental mid-point values. The corrected mean of the F_1 is 130 days with standard error of 12 but from the data of Table II the standard error of 10 genetically uniform seeds on the upper part of the range is calculated at about 30 days. Earlier tests, Stokes and Hull (1930), found the emergence of four F_1 seeds of as many different crosses to be intermediate between that of their parents in each case. It is concluded from the combined F_1 data that the F_1 position is probably slightly above the parental mid-point.

Comparisons of later generation hybrids with their respective parental mid-points are also somewhat indefinite because correction for the errors noted above cannot be made accurately. Means of the greater parents are increased 20 days by correction for delay in planting while corrected means of lesser parents cannot be less than eight nor greater than 28 days. Hybrid means are subject to corrections for both delay in planting and unequal experimental error. The first

correction is an increase of something less than 20 days; the second is a decrease of probably a similar amount. If minimum corrected values of the lesser parents are accepted and no corrections are applied to hybrid means, the corrected parental mid-points exceed the various hybrid generations by 25, 54, -3, 49, 44, 28, 40, and 35 days respectively in the order listed in Table VII. These differences are, with one exception, much greater than any corrections which might belong to the hybrid means. The exception is based on small samples. There can be little doubt that mean rest requirements of later generation hybrids are distinctly lower than the parental mid-points.

Presentation of the behavior of rest period is completed with transgressive segregation. The most striking example is F_2 family No. 63-77, shown at the bottom of Table V. The mean gain of the F_4 seeds of this family over the greater parent is 111 days with standard error of gain of 15. Less marked but probably significant transgressive segregations were obtained in the three other crosses of Spanish and runner strains.

The behavior of rest period in hybrids of unlike parents is unique in that the frequency distributions of later generations are highly skewed, and probably in that the F_1 is nearer to the parental mid-point than are the means of later generation hybrids. Perhaps these two variations from the usual picture are manifestations of a single causal factor.

The data that are partially presented in Table V strongly indicate that some skewness may be caused by the genetic range extending below the zero point of the physical character. If that is the only important cause and the inheritance of rest period is otherwise the familiar quantitative type, normal distributions should occur if the restriction on measuring rest period could be lifted. Distributions of gene frequency and probably of genotype value are normal. Dominance may be neglected in later hybrid generation distributions. All of the samples of later hybrids, except the F_3 of cross (1 x 14), have more than 50 per cent of their frequency on the visible range of rest period. If the upper one-half of each distribution is an undistorted half of a normal distribution, the medians on the physical range approximate the means on the genetic range and the means approximate the parental mid-points. Such calculations place the less dormant parents from 20 to 130 days to the left of the point of no rest requirement at maturity. The genetic range must be extended 110 days or more still farther to the left to allow for transgressive segregation equal to that obtained in the opposite direction. The F_1 is well above the hypothetical mid-point of its parents but its relation to the greater parent is unchanged.

An alternative hypothesis is that seeds of any genotype other than the minimum possess some rest requirement or that the genetic range does not extend farther to the left than

the point of no rest requirement at maturity. The limit might be assumed at any lower point but it seems unnecessary to consider such possibilities for the present. A limit on the genetic range cannot of itself cause skewness but a limit at the point suggested coupled with some special type of gene interaction might have given rise to the present situation. No scheme that is consistent with the data has been discovered nor has it been possible to demonstrate that one does not exist.

The hypothesis that inheritance of rest period differs from the usual quantitative type only in that the zero point of the physical character lies well up on the genetic range seems preferable because of greater simplicity and because it is strongly suggested by the data.

Apparently it will be safe to direct breeding operations as though the hypothesis was correct. Peanut improvement may frequently involve hybridization of Spanish or Valencia strains with runner or other more dormant strains. Strains of hybrid origin may also be used in further crossing. Usually it will be desired to recover as long or even longer rest period than is found in the more dormant parent. Strains of the Spanish and Valencia groups may be expected to have negative breeding values even though they exhibit mean rest periods up to 50 days or more with the present accuracy of testing. Relative breeding values of both less dormant and more dormant strains

may be expected to follow the same order as the tests on their own seeds but the possibility of some combinations proving particularly satisfactory or unsatisfactory cannot be entirely overlooked.

Rest period tests will usually be deferred until later hybrid generations when only a small proportion of selected lines is still retained. The probability of recovering rest requirement in satisfactory amounts in such lines is lessened by the skewed distributions. It is desirable to know what proportion of F_2, F_3, and later generation families may be expected to retain satisfactory rest requirement. A partial answer is found in Table IV, particularly with the distribution of F_3 families. The 944 F_3 plants were tested with an average of 30 F_4 seeds. About five per cent were as great as the greater parent. This five per cent of satisfactory F_3 plants came from 25 per cent of the F_2 plants but five per cent of the F_2 plants contributed nearly one-half of them. It would seem that weak selection, such as might be provided by delaying harvest two or three weeks after maturity, could be helpful in eliminating less dormant types in the earlier generations. However, such practice may not always be feasible. Since 75 per cent or more of genes affecting rest period are probably fixed in the F_3 generation, it is clear that approximately five per cent of later generation lines chosen at random from (1 x 14) crosses may be expected to have as long rest requirement as the greater

parent. Three other crosses have given very similar results in F_3 so it would appear that the conclusion just made might apply in most crosses of more dormant and less dormant strains. The possibility of recovering longer rest period in hybrid strains than is found in the greater parent has been indicated by marked segregation above the greater parents in several crosses.

SEED SHAPE

Spanish peanuts have short, nearly spherical seeds while the seeds of runner peanuts are oblong. Varieties of the Valencia group have seeds somewhat distorted in shape by being closely packed in the many-seeded nuts. Hayes (1933) has reported long seed dominant with a 15:1 ratio in a cross of Valencia with Sine. Sine is a runner variety and was described as short-seeded which is certainly unusual in the runner group.

The F_2 and F_3 plants of crosses (1 x 14), (13 x 14), (3 x 8), and (13 x 8) seemed to fall rather easily into three classes: short-seeded, intermediate, and long-seeded. There was, however, considerable variation in the shape of seeds from any one plant. No attempt was made to classify single seeds because their shape is often slightly distorted. The intermediate group of plants was so truly intermediate that dominance of either shape was not detected. Comparison of the data of the several crosses with an hypothesis of single gene inheritance and no dominance is presented in Table VIII. Agreement with the expected ratios is quite satisfactory throughout.

SEED COAT COLOR

Seed coat color of peanuts varies from dark purple through red, russet, and tan to nearly white. One strain of A. Nambyquarae lacks the outer, pigmented layer of the seed coat and its seeds are paper white. Every report that has appeared thus far on inheritance in peanuts has included 3:1 ratios of red to russet or tan. Other color differences have not been considered. The present study deals with russet and tan as they occur in runner and Spanish peanuts.

The F_2 and F_3 plants in cross (1 x 14) and the F_2 plants of crosses (13 x 14), (3 x 8), and (13 x 8) were classified as having russet, intermediate, or tan seeds. The proportions of intermediates obtained were so small that they were finally combined with the russet classes which had the greater numbers. Russet is clearly dominant but the difference between russet and tan is so slight that correct classification is not easily accomplished in every case. Samples of parent strains of the same year's crop were kept at hand while the classifications were made since the color gradually darkens after the seeds are harvested. Those plants whose seeds were as light as the darkest variations of Spanish parents were classed as tan while the others were finally all classed as russet. The data

are summarized in Table IX and compared with an hypothesis of single gene inheritance with russet dominant which they fit very closely.

YELLOW SEEDLINGS

Badami (1928) reported triplicate gene inheritance of chlorophyll in peanuts with the triple dominant dark green and the triple recessive albino. The statement suggests that the double and single dominants were lighter green than the triple.

Yellow seedlings in the present case were probably controlled by duplicate genes with green fully dominant and the yellow plants sometimes showing faint traces of green. It is unlikely that these yellow seedlings are identical with the albinos which Badami observed.

Crosses involving five strains of Spanish, four of runner, four from the Valencia group, and one each from A. Nambyquarae and A. Rasteiro have been studied. All crosses of Spanish x runner have produced yellow F_2 seedlings. No crosses involving the Valencia group of A. Rasteiro have produced them. A. Nambyquarae has behaved as the runner group. It has been learned through correspondence with Dr. L. Husted, University of Virginia and Dr. B. B. Higgins, Georgia Experiment Station that these results have been confirmed with a number of crosses involving the Spanish, runner, and Valencia groups in their cultures. Hayes (1933) reported a cross of Valencia with a runner strain but noted no yellow plants.

Yellow seedlings have not appeared in F_1 and only in low frequency in F_2 but with greater frequency in the F_3 of some families. This evidence strongly suggested duplicate gene inheritance with green dominant and also that the genotypes $L_1L_1l_2l_2$, $l_1l_1L_2L_2$, and $L_1L_1L_2L_2$ might be assigned respectively to the Spanish, runner, and Valencia groups of peanuts. Inheritance studies of yellow seedlings have been made principally in four crosses involving Spanish and runner strains. The data of the cross (1 x 14) which was studied most extensively are presented in Table X. It soon became apparent that very few families appeared in this or other crosses with ratios as low as 3:1. Consequently a few F_3 progenies were selected because of low ratios in seedling progeny tests with the expectation that only monohybrid plants would be included. These were continued another generation and seedling tests were made on F_4 plants. The ratios of true and segregating F_4 families, and green and yellow F_5 seedlings are shown in the last two entries of the table. The deficiency of yellows in the F_5 test is too great to be ascribed to chance nor can it be explained by differential germination since the segregating families germinated equally with their sibs. Since the deficiency appeared in monohybrid families, it could not be due to linkage of duplicate genes. Other possible causes, e.g. abnormal behavior at meiosis, must become evident in unequal numbers of effective gametes or in differential viability of zygotes.

An attempt was made to determine as closely as possible gametic ratios of both sexes and differential viability of zygotes. It was assumed after a preliminary inspection of the data that gametes containing one or more dominant genes were produced in equal numbers and were equally viable. The ratio of fully recessive gametes to those of any one dominant class was defined as q. The gametic proportion for one sex of the monohybrid was then written

$$\frac{1}{1+q} + \frac{q}{1+q} = 1$$

and for the dihybrid

$$\frac{1}{3+q} + \frac{1}{3+q} + \frac{1}{3+q} + \frac{q}{3+q} = 1$$

Identical equations with q' served for the other sex in both cases. It was further assumed that zygotes with one or more dominant genes were equally viable and that the ratio of viabilities of dominant and recessive zygotes was (1:w).

Defining:

T = recorded number of dominant progeny breeding true,

S = recorded number of dominant progeny segregating,

Y = recorded number of recessive progeny,

and omitting intermediate steps, it is possible to write for the case of self-fertilization of a monohybrid,

$$q + q' = \frac{S}{T}$$

$$qq' = \frac{Y}{T} \cdot \frac{1}{w}$$

and for a dihybrid

$$q + q' = \frac{7S}{3T} - \frac{2}{3}$$

$$qq' = \frac{7Y}{T} \cdot \frac{1}{w} .$$

It is of no advantage to treat the dihybrid and monohybrid progeny of the dihybrid separately since they do not provide independent equations. Also they cannot be separated accurately without extensive progeny tests. They are combined in 3 for this study. The best solutions obtained for these two pairs of equations are the pairs of quadratic roots:

$$q \text{ or } q' = \frac{\frac{S}{T} \pm \sqrt{\left(\frac{S}{T}\right)^2 - 4\,\frac{Y}{Tw}}}{2}$$

and

$$q \text{ or } q' = \frac{\frac{7S}{3T} - \frac{2}{3} \pm \sqrt{\left(\frac{7S}{3T} - \frac{2}{3}\right)^2 - 28\,\frac{Y}{Tw}}}{2}$$

In neither case has the necessary third condition or equation to solve for three unknowns been found but the situation is not entirely hopeless. Since the roots cannot be complex the discriminant cannot be less than zero. Setting it equal to zero provides a minimum limit on w in each case. Also the

maximum limit on the larger root may be reasonably taken at one thus setting a maximum limit on w. Taking these limits for the monohybrid,

$$\text{Max. } w = \frac{Y/T}{(S/T - 1)}, \qquad \text{Min. } w = \frac{4\ Y/T}{(S/T)^2}$$

and for the dihybrid

$$\text{Max. } w = \frac{21\ Y}{(7S - 5T)}, \qquad \text{Min. } w = \frac{28\ Y/T}{(7S/3T - 2/3)^2}$$

It should be noted, however, that these limits may be strictly imposed only on expected values of w. Random deviations beyond the limits may readily occur. The entire mathematical treatment given here deals expressly with expected values. Utility of the solutions obtained must be judged by their sampling variances finally. These limits set on w have proven to be of considerable value in the analysis of the present case while further treatment has been fruitless. However, it seems desirable to present the further treatment briefly because accurate evaluations of q, q', and w should prove of great value preliminary to cytological investigations of such cases as the present one.

The segregating F_2 plants from a dihybrid F_1 are dihybrids and monohybrids in the proportions

$$\frac{2 + q + q'}{2 + q + q' + 2(q + q')} + \frac{2(q + q')}{2 + q + q' + 2(q + q')} = 1$$

It seemed that this relation might provide the necessary third condition for a definite solution for q, q', and w in the F_3 generation. Such data were available with cross (1 x 14). However, it was learned from the Jacobian determinant that no solution was possible. This test was kindly made by Dr. L. W. Gaddum of the Florida Experiment Station, who then suggested that a combination of the data in three separate cases should provide three independent equations and a definite solution for q, q', and w. The first choice for this attack was the ratio of recessives to the total number of progeny in each of three cases since the error involved in experimentally determining these ratios is least. Classification into true breeding and segregating is hazardous unless very large progenies are grown. The ratios of recessive to total progenies in a monohybrid, a dihybrid, and in the F_3 progeny of segregating F_2 plants from a dihybrid F_1 were designated as a, b, and c respectively. Solution of the three equations resulted in:

$$q + q' = \frac{9b - 8ab - a}{a + 2ab - 3b}$$

$$qq' = \frac{3ab}{(a + 2ab - 3b)w}$$

$$w = -\frac{c(b-2ab+a)(21b-20ab-a)}{c(1-a)(1-b)(21b-20ab-a)} \\ \frac{- b(a-2ac+c)(3b-4ab+a) - 2a(b-2bc+c)(9b-8ab-a)}{- b(1-c)(1-a)(3b-4ab+a) - 2a(1-c)(1-b)(9b-8ab-a)} .$$

These formulae are apparently correct mathematically. They work perfectly with hypothetical cases when no deviations from expected values are allowed. Deviations in any one of the ratios, a, b, or c which have 50 per cent probability with samples of 500 to 1000 throw the results entirely out of line. The formulae are of very limited utility, presumably because of enormous size of their sampling variances. Similar formulae might be calculated from the ratios of segregating to total progeny, or to true breeding progeny, or from any set of three independent equations involving the three unknowns. None of these other possibilities have been investigated fully as yet, but the probability of finding a more valuable set of formulae appears to be very small.

Estimates of q, q', and w were obtained by calculating maximum and minimum w in the dihybrid F_3 and the monohybrid F_4 families of cross (1 x 14) by the formulae given above. For the F_3 maximum w is 0.82 and minimum w is 0.79 while for the monohybrid F_4 families maximum w is 0.76 and minimum w is 0.73. In either case, for maximum w, q = 1.00, q' = 0.66; while for minimum w, q = q' = 0.83. The corrected ratios in Table X have been based on an hypothesis of q = q' = 0.83, and w = 0.75. There is, unfortunately, no evidence for or against equality of q and q'. The ratios of F_3 seedlings, F_3 families, F_4 families, and F_5 seedlings were used to build the hypothesis and are not entirely independent of it. Tests of the

hypothesis lie in the ratios of F_3 seedlings, F_3 families, and F_4 seedlings which data were not used to calculate q, q', and w.

Theoretical ratios for later generations were also corrected for random deviations and differential productivity in earlier generations. The ratio of F_3 families was, in addition, corrected for the proportion of dihybrid families expected to produce no recessive progeny and apparently breed true because of few progenies tested. Contributions of these factors to X^2 must of course be eliminated if a fair test of the hypothetical values of q, q', and w is to be obtained.

It was possible to make the above corrections on the theoretical F_3 ratio with reasonable assurance. This ratio is presented in Table XI for the entire population and for the progenies of dihybrid and monohybrid F_2 plants separately. Good fits were obtained in all cases. The ratios of F_3 families and F_4 seedlings could not be corrected so accurately and the fits obtained were hardly within the limits of random sampling. However, judging the data of Table X as a whole, there can be little doubt that the hypothesis of duplicate genes with deficiencies of recessive gametes and zygotes is correct. It is also indicated that the calculated values of q, q', and w which are measures of those deficiencies are not greatly in error, at least in their resultant.

Records of yellow seedlings in the other three crosses are available only for the F_2 and F_3 generations. These data

are sufficient only to set limits on w and to approximate q and q'. In cross (13 x 14) there were 82 F_2 seedlings of which 64 green plants were grown to maturity and tested for segregation with 4,479 F_3 seedlings. By the formulae given above for a dihybrid, maximum w is 0.91 and minimum w is 0.84. Taking the maximum value of w, q = 1 and q' = 0.57. Taking the minimum value of w, q = q' = 0.78.

In cross (3 x 8) there were 212 F_2 seedlings from three F_1 plants of which 198 were grown to maturity and tested for segregation with 13,781 F_3 seedlings. Maximum w is 0.727 and minimum w is 0.723. For minimum w, q = q' = 1.08. In this cross the proportion of segregating plants is slightly in excess of the expected proportion with q = q' = 1. There is no evidence of deficiency in q or q'.

In cross (13 x 8) there were 146 F_2 seedlings of which only two were yellow. However, the occurrence of yellow plants among 6,174 F_3 seedlings from 121 F_2 plants is very similar to that of the previous cross. The unusual F_2 result prevents any reasonable determinations of limits on w as in previous crosses. The proportion of segregating F_2 plants is very close to that expected with q = q' = 1. There is no evidence of deficiency in q or q'. Two estimates of w have been made from the ratios of green to yellow plants in the F_3 derived from the segregating F_2 plants and in the total F_3. In these two cases the proportions of yellow plants are 0.73 and 0.74 of

that expected with q, q', and w equal to one. This deficiency must be largely ascribed to w, and the ratios of yellow plants obtained to the numbers expected with a hypothesis of w equal to one may be considered estimates of w.

Values of q, q', and w obtained in the first two crosses are quite similar. These crosses involve runner strain No. 14 crossed with the Spanish strains No. 1 and No. 13. The latter two crosses also behaved similarly but different from the first two. They involve runner strain No. 8 crossed with Spanish strains No. 3 and No. 13. Deficiencies in q and q' would appear to be associated with strain No. 14. The significance of these deficiencies especially in q and q' in relation to abnormal associations in meiosis noted by Husted (1933) must not be overlooked. However, they would seem to be adequately and more simply explained by a weakening effect of the recessive genes in both the gametic and zygotic stages. Examination of pollen in monohybrid families has discovered no plants with less than 95 per cent of normal appearing grains and little variation in the amount of aborted pollen. Segregating plants are frequently slightly less productive than true breeding, green plants. However, no significant differences between true green, dihybrid, and monohybrid F_3 plants or families have been found. It is possible that the indeterminate blooming and fruiting habit of the plant enables it to eliminate largely the effect of a considerable proportion of aborted ovules.

VALENCIA PLANT TYPE

It was stated above that the Valencia group of peanuts is different from other American types in its very sparse branching habit and by commonly producing three or four seeds in a nut. Chevalier (1933) has assembled the varieties having many-seeded nuts into a principal variety, stenocarpa. He lists Tennessee Red and Tennessee White but omits Valencia which, as known in America, should be included as should Porto Alegre from Brazil. Chevalier also describes two African forms with many-seeded nuts. One is stated to have few branches which are long, slender, and prostrate. Both are low yielding which is a common character of sparsely branched types. Perhaps both are sparsely branched. If so, sparse branching and many-seeded fruits are constantly associated in all known varieties which possess either character. The two characters have appeared to assort independently in crosses of Valencia or Tennessee Red with Spanish or runner strains.

Sparsely branched peanuts frequently have a central stem or rachis in the fruiting cluster up to several inches in length. Sometimes a few small leaves are found at the tip. Fruit stalks are borne singly and alternately along this stem. The typical inflorescence of peanuts as described by botanists

and found in other forms is a reduced head. The fruit cluster consists of one to four ovary stalks with sessile attachment. Plants having the central stem in the fruiting cluster and sparse branching habit have been found among the later generations of crosses between Spanish and runner peanuts. Such plants do not have many-seeded fruits necessarily. Their analogy with Valencia type is not easily recognized at first because of their usually long, slender, prostrate branches. Valencia and related varieties except the African forms described by Chevalier have short, thick, upright branches. The type of hybrid plants with sparse branching and central stem in the fruit cluster has been named Valencia plant type. There is no inference as to the number of seeds per nut.

The inheritance of Valencia plant type has not been investigated in crosses involving any varieties of the Valencia group but the data of a cross of Spanish and Jumbo Runner, (1 x 14), are summarized in Table XI. The record on the F_2 is not known exactly but it is certain that approximately five per cent were Valencia type as was the case in other crosses of Spanish and runner peanuts. When the F_3 generation of cross (1 x 14) was grown the significance of the sparsely branched plants was recognized. Seventy-two F_3 families were grown to maturity with an average of 13 plants. The occurrence of Valencia type plants suggested duplicate gene inheritance with Valencia type recessive. Theoretical ratios based

on that hypothesis are compared with the experimental ratios in Table XII. Because of the small number of F_3 plants in the F_2 families it was necessary to correct the theoretical ratios. This was done by making use of Warwick's tables (1932). In the portion of the table dealing with 13 progeny tested, it is recorded that 43 per cent expected to breed 15:1 would produce no recessive progeny while the other 57 per cent are expected to produce dominants and recessives in a ratio of 8.085:1. These corrections were made on the theoretical ratios in the first and second comparisons of Table XI. No correction for the monohybrid families was necessary. These corrections are not entirely accurate since the number of F_3 progeny per F_2 was not constantly 13. A more accurate correction could probably be made by treating each F_3 family separately and summing the corrections. However, the error in the method used tends to increase X^2 and no false conclusions are likely.

Agreement of the data with the hypothesis is quite satisfactory in three comparisons. It is concluded that Valencia type is a recessive character controlled by duplicate genes. Peanut varieties of the Valencia group are probably of the genotype va_1 va_1 va_2 va_2 while Spanish may be assigned Va_1 Va_1 va_2 va_2 and runner peanuts va_1 va_1 Va_2 Va_2. The classification of peanut varieties proposed and used here may thus be given additional support.

BRACHYTIC DWARF PLANTS

Brachytic dwarf plants were discovered in a field planting of one F_3 family of a cross of Virginia Runner with Tennessee Red. Five other F_3 families of the same cross did not show the character nor has it appeared in any other cultures although a number of related hybrids has been grown. The six dwarf plants had greatly shortened internodes, and the leaf rachis was shortened so that the two pairs of leaflets were found in a cluster. This was true of first seedling leaves and of later leaves on the plant. Blossoms were reduced in size with anthers containing mostly empty pollen grains. Occasionally a few fruit stalks developed to a length of an inch or more but no fruit development was found.

One of the segregating, normal sibs of the dwarf plants was carried through another generation and seedling tests made on 17 of its progeny. Five of them bred true and 12 segregated. The 12 segregating plants produced 393 normal to 114 dwarf seedlings. For the test of this ratio against a theoretical 3:1, $X^2 = 1.71$, $P = 0.18$. One of these segregating plants was tested a generation further, producing seven true breeding progeny and 20 segregating. The 20 segregating plants produced 394 normal and 139 dwarf seedlings. For the

test of this ratio against a theoretical 3:1, $X^2 = 0.33$, P = 0.58. Combining the numbers breeding true and segregating in the two tests produces a ratio of 12:32. Testing this ratio against a theoretical 1:2, $X^2 = 0.73$, P = 0.40. Brachytic dwarf behaved as a single recessive character.

REGRESSION TESTS

Records of the 22 characters listed in the first column of Table XII were taken in the F_2, F_3, or F_4 generations of cross (1 x 14). Records on nearly all of the same characters were taken in the F_2 or F_3 generations of crosses (13 x 14), (3 x 8), and (13 x 8). Those characters which did not fall naturally into definite classes were graded numerically. The F_3 and F_4 records were then averaged by F_2 families and only F_2 values were used in regression tests. The tests were made by the analysis of variance and z test of Fisher (1930) as modified by Snedecor (1934). Regressions of the several characters listed on rest period, seed shape, seed coat color, and yellow seedlings were tested in all four crosses and, in addition, regressions on Valencia plant type were tested in cross (1 x 14). Regression is used here in the broad sense to refer to any type of association or dependence between variables.

The classification of rest period given above produced highly skewed distributions not well suited to analysis of variance tests. That method of classifying was called "equal interval" because all class intervals were equal except the first which was of indeterminate breadth in the genetic sense. Transformations of the distributions were made by two other methods of classification. It was necessary in making these

transformations to assume that the relative rank of F_8 mean rest periods was measured with reasonable accuracy. However, no doubt need be entertained of significant regressions on that account since failure to classify correctly could hardly produce spurious regression.

The first transformation was to a rectangular distribution by taking classes of equal frequency throughout. This provided tests of regression on rank. The second transformation was an attempt to normalize the distributions by taking class frequencies proportional to areas of equal breadth under the normal curve. It was done by dividing a range of 2.6 standard deviations plus or minus into equal sections and calculating the proportionate frequencies from Fisher's Table I (1930). The total range of 5.2 standard deviations centered at the mean includes a little more than 99 per cent of the total area under the normal curve. Justification for this transformation lies in the supposition that distributions of rest period genotypes are probably not far from normal type.

Most of the tests on rest period were made with the transformed rectangular distributions but a few tests with the other distributions are also shown in Table XII. When rest period served as the dependent variable only the actual data were used with no transformation and no transformations of distributions of other variables were made in any case.

Values of F for the several tests of regressions on rest period in cross (1 x 14) are presented in Table XII. The F values for tests of regression on seed shape, seed coat color, yellow seedlings, and Valencia plant type of the 22 recorded characters in the four crosses have been omitted. As shown by the column headings each series of F values is listed in two columns, "Between" and "Within", to indicate which was the larger mean square in the ratio F. A significantly greater between mean square indicates that increasing variance of the independent variable has entailed increasing variance of the dependent variable and may be interpreted as proof of regression. A greater within mean square indicates that the group means of the dependent variable are more alike than expected with random sampling. Values of F for the points of five and one per cent probability, Snedecor (1934), are given at the bottom of each column and all values of F in the table which exceed the five per cent point have been underscored.

The F values of tests of the regressions of the two generation measures of rest period on each other are highly significant with each of the three methods of classification when judged by the criteria applicable with normal distributions. That they are really significant seems probable from a comparison with other F values in the table which range much smaller generally. The F values of the other tests which were not listed were also much smaller. Significant regressions of the

different generations of rest period on each other were to be expected since strong heritability of the character was already demonstrated. Perhaps the principal value of these tests was to provide F values derived from highly skewed distributions with strong regressions to compare with other F values also derived from highly skewed distributions where the order of regression was unknown.

Some of the characters other than rest period also had highly skewed distributions. Seed coat color was classified sometimes in ratios approximating 1:2:1 and in other cases the ratios approximated 3:1. Valencia plant type has a highly skewed distribution in cross (1 x 14) as may be seen in the first experimental ratio of Table XI. This character is controlled by duplicate pairs of genes with one pair coming from each parent of the cross; thus it is hardly expected that genetic regressions involving Valencia plant type should be found in F_2. The order of F values obtained with characters having skewed distributions appears not different from that of characters whose distributions are generally symmetrical.

Only a few of the F values obtained in tests involving two separate characters exceed the points of significance and those few to no great extent. Results of the several tests on any pair of characters are frequently inconsistent or contradictory. It might appear, e.g., in Table XII that greater between mean squares were obtained too frequently with both

plant weight and weight of nuts to be ascribed to chance but in the other three crosses no significant F values were obtained and the between mean squares were as often smaller as greater than the within.

It is concluded that any regressions which exist between the characters tested must be weak. The significant values of F which appeared are more probably due to non-normal distributions, to errors which may have occurred in recording and calculating the data, or to the sampling variance of F itself.

The probability of strong genetic regressions, especially with quantitative characters, in the peanut must be small. The number of chromosomes is large, 20 haploid. Also polyploidy, probably tetraploidy, has been suggested by the cytological findings of Husted (1933) and by the several pairs of duplicate genes which have been reported by Hayes (1933) or in the present paper. Since no strong genetic regressions were uncovered it would seem that rigid selection for rest period, seed shape, seed coat color, and probably most other characters might be practiced with little fear of accumulating undesirable genes. The possibility of finding linked markers of rest period is almost entirely eliminated.

SUMMARY AND CONCLUSIONS

Peanut seeds planted soon after maturity in conditions near optimum for germination frequently required rest periods ranging up to two years before germinating. Rest periods were apparently due to necessary physical or chemical changes within the seeds which comprise a process commonly called "after-ripening".

The average time to emergence of different strains from the Spanish and Valencia groups of peanuts ranged from 9 to 50 days while in a more dormant group including runner peanuts, A. Nambyquarae, and A. Rastoiro it ranged from 110 to 210 days. Genetic differences between strains within the two groups were demonstrated to be very probable.

Frequency distributions of time to emergence in pure strains and hybrid populations were highly skewed to the left with modes at the point of zero days rest period in most cases. The degree of skewness was greater in less dormant samples. Intermediate samples had two modes, one of which was at zero, while the most dormant samples had single modes near the centers of nearly symmetrical distributions.

The mean time to emergence of F_1 seeds was intermediate and probably slightly greater than the average of the parents.

Means of later generation hybrids were considerably below the mid-points of their parents.

Marked transgressive segregation of F_2 families above the greater parents was found in four crosses of Spanish and runner peanuts. These segregations were thought to indicate the presence of considerably more genic material in the less dormant parents than was evident in their own rest period tests and that a large part of this genic material was different from any found in the more dormant parents.

The data on rest period suggested an hypothesis of rest period inheritance being the familiar quantitative type with slight dominance of long rest period and a single qualification that the zero point of the physical character might be found well up on the genetic range.

A single pair of major genes differentiating long and short seeds with the heterozygote intermediate was demonstrated in crosses of Spanish and runner peanuts. The results indicated that seed shape was controlled largely by maternal impression and very little by the genotype of the seed.

Russet seed coat color of runner peanuts behaved as a single dominant to tan color of Spanish peanuts.

Yellow seedlings appearing among progenies of a number of crosses indicated duplicate gene inheritance with green fully dominant. It was also indicated that the genotypes $L_1L_1l_2l_2$, $l_1l_1L_2L_2$, $L_1L_1L_2L_2$ might be assigned respectively to the

Spanish group, to the runner group and A. Nambyguarae, and to the Valencia group and A. Rasteiro. Deficiencies of recessive zygotes were found in both monohybrid and dihybrid progenies in all crosses and in some cases deficiencies of segregating plants in proportion to true breeding dominants were also found. An attempt to calculate the deficiencies of recessive zygotes and of recessive gametes in both sexes was only partially successful. No explanation of the deficiencies other than lower vigor of recessive gametes and zygotes was discovered.

Valencia plant type, so named from its similarity to the sparse branching habit of Valencia peanuts, was found among the progenies of several crosses of Spanish and runner strains. It behaved as a duplicate gene recessive indicating that the parent groups carry alternate pairs of duplicate genes in the recessive and dominant conditions.

A division of the American varieties of A. hypogaea into three principal groups: runner, Spanish, and Valencia was proposed and used in the present study. It was supported not only by morphological characteristics but also by the distribution of duplicate genes controlling yellow seedlings. Probability that the distribution of duplicate genes controlling Valencia plant type also supports the classification was indicated.

Male-sterile, brachytic, dwarf plants were discovered in one F_2 family of a cross of Virginia Runner and Tennessee Red. The character behaved as a monogenic recessive.

Analyses of variance of the 22 characters listed in the first column of Table XII within and between rest period of seeds, seed shape, seed coat color, yellow seedlings, and Valencia plant type were computed. The tests were made with F_2 plants or families in four crosses of Spanish and runner peanuts. From the results of these analyses of variance, it was concluded that no significant regressions were present.

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TABLE I

Frequency distributions, means, standard errors, and variances of days from planting to emergence with numbers tested and germination percentages in rest period tests on less dormant, pure strains of peanuts. (Frequencies expressed by percentage)

Pedigree numbers	Class limits						
	6	17	37	57	77	97	117
1*-31**	98.9	1.1					
	100.0						
1-32	97.0	1.0		1.0			
	91.7	8.3					
7-32	92.7	2.8	1.8	1.8			
	92.3		7.7				
12-31	92.9	2.0	1.0	2.0	1.0		
	90.0	10.0					
6-31	90.2	6.5	1.1	1.1	1.1		
	100.0						
4-31	96.5			1.2			
	90.0	10.0					
3-31	79.6	3.1	1.0	7.1	4.1	2.0	
	40.0	50.0	10.0				
7-31	75.8	5.3	3.2	2.1	5.3	1.1	
	30.0	40.0	30.0				
13-31	63.6		2.0	5.1	5.1	2.0	
	10.0	30.0	20.0	30.0	10.0		

*Origin of different pedigrees given on page 9.

**The second figure of each pedigree indicates the year of the test, e.g. 1-31 refers to the 1931 crop of strain No. 1.

The first line after each pedigree number includes the data on single seeds; the second line includes the same data averaged by mother plants.

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127	137	157	177	Number tested	Mean	S.E.	Variance	Germination
				88	9	1	132	91
				10				
	1.0			105	11	2	360	88
				12				
.9				109	11	2	381	90
				13				
.0				99	12	2	254	99
				10				
				92	12	2	210	92
				10				
	2.3			86	14	3	589	86
				10				
2.0	2.0		1.0	98	24	4	1190	98
				10				
1.1 3.2	3.2	1.1		95	28	4	1543	96
				10				
2.0 8.1	8.1	5.1	1.0	99	50	2	427	99
				10				

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TABLE II (a)

Frequency distributions, means, standard errors, and variances of days from planting to emergence with numbers tested and germination percentages in rest period tests on more dormant, pure strains of peanuts. (Frequencies expressed by percentage)

Pedigree numbers	Class limits						
	6	17	57	97	137	177	
21*-32**	8.6	5.7	20.0	51.4	8.6		2.9
			50.0	33.3	16.7		
14-32		0.8	6.9	47.3	26.0	16.0	3.1
				40.0	60.0		
14-31	2.4	12.2	31.7	12.2	19.5	19.5	2.4
				20.0	60.0	20.0	
15-31	4.3	4.3	8.7	13.0	34.8	21.7	8.7
				16.7	50.0	33.3	
11-31	3.1	1.0	13.3	15.3	40.8	14.3	4.1
				30.0	40.0		30.0
8-31	1.0	1.0	3.0	10.1	20.2	40.4	7.1
					30.0	20.0	30.0

*Origin of the different pedigrees given on page 9.

**The second figure of the pedigree indicates the year of the test, e.g. 21-32 refers to the 1932 crop of strain No. 21.

The first line after each pedigree number includes the data on single seeds; the second line includes the same data averaged by mother plants.

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	257	297	337	377	417	457	497	Numb test
	2.9	2.9						35
16.0	3.1							13
								1
19.5	2.4							4
20.0								
21.7	8.7	4.3						2
33.3								
14.3	4.1	2.0				1.0	5.1	9
	30.0							1
40.4	7.1	9.1	1.0		2.0	3.0	4.0	9
20.0	30.0	20.0						1

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7	377	417	457	497	Number tested	Mean	S.E.	Variance	Germination %
					35	112	11	3942	63
					6				
					131	136	4	2482	63
					10				
					41	154	12	5721	91
					5				
					23	161	17	6792	77
					6				
			1.0	5.1	98	170	9	8066	98
					10				
		2.0	3.0	4.0	99	210	11	12451	99
					10				

TABLE II (b)

Comparisons of more dormant strains of peanuts by mean differences and their standard errors. (Underscored differences are thought to be significant as judged by their standard errors and the germination of the two lots).

Pedigree	14-32		14-31		15-31		11-31		8-31	
21-32	<u>24.0</u>	11.4	<u>42.4</u>	15.9	<u>49.1</u>	20.2	<u>58.9</u>	13.9	<u>98.5</u>	15.4
14-32					25.1	17.7	34.9	10.0	<u>74.5</u>	12.0
14-31					6.7	20.8	16.5	14.9	<u>56.1</u>	16.3
15-31							9.8	19.4	49.4	20.5
11-31									<u>39.6</u>	14.4

TABLE III

Frequency distributions, means, standard errors, and variances of days from planting to emergence with numbers tested and germination percentages in rest period tests on less dormant and more dormant pure strains of peanuts and their F_1 and F_2 hybrids. (Frequencies expressed by percentage)

Pedigree numbers	Class limits						
	6	17	57	97	137	177	217
3X		75.0	10.0	10.0		5.0	
221		No test					
(3X x 221)F_1				50.0	20.0	30.0	
7**-31		81.1	5.3	6.4	6.4	1.1	
		70.0	30.0				
7-32		95.5	3.6		0.9		
		92.3	7.7				
3-31		82.7	8.1	6.1	2.0	1.0	
		90.0	10.0				
21-32		8.6	5.7	20.0	51.4	8.6	
				50.0	33.3	16.7	
14-31		2.4		12.2	31.7	12.2	19.5
					20.0	60.0	20.0
(7 x 21)F_2		44.7	23.4	19.1	11.7		1.2
			80.0	20.0			
(7 x 14)F_2		32.5	44.5	16.8	5.2		1.0
		16.7	83.3				
(3 x 21)F_2		14.9	34.0	27.7	21.3	11.7	4.3
			33.3	66.7			

*Estimated from the behavior of other dormant strains.

**Records of parent strains repeated from Tables I and II.

The first line after each pedigree number includes the data on single seeds; the second line includes the same data averaged by mother plants.

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its				Number tested	Mean	S.E.	Variance	Germination %
137	177	217	257					
5.0				20	25 (112-210)*	12	2653	100
30.0				10	110	12	1333	100
1.1				95	20	4	1543	96
				10				
				109	11	2	381	90
				13				
1.0				98	24	4	1190	98
				10				
8.6		2.9	2.9	35	112	11	3942	62
16.7				6				
12.2	19.5	19.5	2.4	41	154	12	5721	91
60.0	20.0			5				
	1.2			94				
				5	45	4	1841	79
	1.0			191	37	2	1083	86
				6				
11.7	4.3			94	73	5	2523	76
				3				

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Tables I and II.

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TABLE IV

Frequency distributions, means, standard errors, and variances of days from planting to emergence with numbers tested and germination percentages in rest period tests on F_3 and F_4 seeds in cross (1 x 14). (Frequencies expressed by percentage)

Pedigree numbers	Class						
	6	17	67	117	167	217	26
1-31*	98.9 100.0	1.1					
1-32	96.2 91.7	1.9 8.3	1.0		1.0		
14-31*	2.4	2.4	22.0 20.0	24.4 40.0	31.7 40.0	17.1	
14-32		3.8	29.8 10.0	47.3 90.0	13.7	5.3	
(1 x 14)							
F_3 means of F_3 progeny	34.7	48.6	9.7	4.2	1.4		
F_4 means of F_4 progeny	18.1	58.3	19.4	2.8		1.4	
F_3 single seeds	60.2	19.4	11.7	5.4	1.6	0.4	0.4
F_3 means of F_4 progeny	30.3	47.6	14.7	3.8	1.9	0.4	0.3
F_4 single seeds	49.6	28.0	9.8	8.3	2.0	0.7	0.5

*Records of the parent strains repeated from Tables I and II.

	Class limits						
26'	317	367	417	467	517	567	617
17.1							
5.3							
					1.4		
1.4							
0.4	0.4				0.2		0.4
0.4	0.3	0.7	0.2				
0.7	0.5	0.3	0.2	0.2	0.1	0.1	0.1

II.

567	617	667	717	Number tested	Mean	S.E.	Variance	Germination %
				88	9	1	132	90
				10				
				105	11	2	360	88
				12				
				41	154	12	5721	91
				5				
				131	136	4	2483	63
				10				
				72	42		3889	
				72	47		1819	
	0.4		0.2	495	42	3	4937	93
				944	47		3074	
0.1	0.1	0.1		31029	39	1	4172	91

TABLE V

Frequency distributions and means of days from planting to emergence with numbers tested and germination percentages in rest period tests on F_4 seeds of a representative sample of F_3 families in cross (1 x 14).
(Frequencies expressed by percentage)

F_3 plant numbers	Class limits							
	6	17	67	117	167	217	267	317
97	97.6	2.4						
10	99.0	1.0						
78	91.5	6.2	1.6	0.7				
55	72.6	21.7	4.7	0.7	0.3			
39	75.0	17.4	7.6					
103	80.3	13.4	3.4	2.2	0.4	0.4		
21	72.8	19.2	6.4	1.5	0.1			
98	56.6	34.3	7.4	1.4		0.2	0.2	
56	72.0	12.0	7.6	6.2	1.4	0.2	0.5	
71	60.6	22.3	12.3	4.4	0.2		0.2	
66	49.4	35.7	6.6	6.0	1.1	0.2	0.4	0.6
69	39.9	28.6	13.0	17.6	0.8			
94	30.2	45.4	15.4	6.9	1.3	0.5	0.2	
46	28.9	41.6	11.6	15.9	1.6	0.2	0.3	
60	32.5	31.6	12.6	16.5	2.2	0.3	2.0	0.8
27	19.0	30.1	17.2	26.9	5.0	1.1	0.3	
24	20.4	39.8	15.0	14.3	4.2	2.6	0.3	0.8
53	20.8	8.7	10.3	37.4	13.7	4.7	2.9	0.8
75	5.3	23.7	19.8	33.5	9.6	3.0	0.9	0.9
77	6.7	4.8	10.3	17.9	10.9	5.1	6.7	7.1

317	367	417	467	517	567	617	Number tested	Mean	Germ nati %
							596	8	90.
							196	8	72.
							723	12	95.
							749	19	95.
							212	20	95.
							269	21	72.
							781	23	97.
2							566	27	84.
5							784	30	95.
2							942	35	91.
4	0.6						545	39	97.
							607	44	95.
2							632	51	86.
3							895	60	95.
0	0.8	0.8		0.6			357	71	93.
3		0.3					379	77	76.
3	0.8	0.5	0.5	0.8			622	90	92.
9	0.8		0.3		0.3		384	115	96.
9	0.9	0.7	1.0	0.4			565	123	92.
7	7.1	4.2	8.3	4.5	6.1	4.5	2.6	312	265	84.

TABLE VI

Analyses of variance of days from planting to emergence in the F_4 seeds of two most dormant F_3 families from cross (1 x 14).

Source of variation	Degrees of freedom	Sum of squares	Mean square
F_3 family, 63-75			
Total	564	4,541,066.62	8,051.54
Between F_3 families	16	978,490.15	61,155.63
Within	548	3,562,576.47	6,501.05
F* = 61,155.63/6,501.05 = 9.41; $F_{(0.05)}$ = 1.6, $F_{(0.01)}$ = 2.0			
F_3 family, 63-77			
Total	311	10,085,143.59	32,428.11
Between F_3 families	12	850,112.33	70,842.69
Within	299	9,235,031.26	30,886.39
F* = 70,842.69/30,886.39 = 2.29; $F_{(0.05)}$ = 1.79, $F_{(0.01)}$ = 2.24			

*$F = \frac{\text{larger mean square}}{\text{smaller mean square}}$, Snedecor (1934).

TABLE VII

Summary of means of days from planting to emergence in rest period tests on less dormant and more dormant, pure strains of peanuts and their hybrids.

Cross	Less dormant parent	More dormant parent	Mean of parents	F_1	F_2	F_3	F_4
3X* x 221	25	(112-210)**	(68-118)	110			
7 x 21	19	112	65		45		
7 x 14	19	154	87		37		
3 x 21	24	112	68		73		
1 x 14	10	154	82			42	47
13 x 14	50	154	102			63	
3 x 8	24	210	117			79	
13 x 8	50	210	130			84	

*Two sister plants from strain No. 3 were used as parents for the ten F_1 seeds and were labeled 3X. Origins of the different pedigrees are given on page 9.

**No test was obtained on strain No. 221 due to constantly poor quality of its seeds but it is undoubtedly a more dormant type.

TABLE VIII

Summary of inheritance of seed shape in crosses (1 x 14), (13 x 14), (3 x 8) and (13 x 8).

Pedigree	Short	Inter-mediate	Long	N	X^2	P
63 F_2						
Observed	52		20	72		
Theoretical(3:1)	48		16		0.29	0.59
63 F_3 families						
Observed	25	29	18	72		
Theoretical(1:2:1)	18	36	18		4.08	0.14
63 F_3						
Observed	596		348	944		
Theoretical(5:3)	590		354		0.18	0.66
68 F_2						
Observed	16	32	16	64		
Theoretical(1:2:1)	16	32	16		0.00	1.00
71 F_2						
Observed	54	97	47	198		
Theoretical(1:2:1)	49.5	99	49.5		0.58	0.75
74 F_2						
Observed	31	60	30	121		
Theoretical(1:2:1	30.25	60.50	30.25		0.02	0.90

TABLE IX

Summary of inheritance of seed coat color in crosses (1 x 14), (13 x 14), (3 x 8) and (13 x 8)

Pedigree	Russet	Inter-mediate	Tan	N	X^2	P
63 F_2						
Observed		50	22	72		
Theoretical(3:1)		54	18		1.20	0.28
63 F_3 families						
Observed	22	30	20	72		
Theoretical(1:2:1)	18	36	18		1.44	0.49
63 F_3						
Observed		564	380	944		
Theoretical(5:3)		590	354		3.20	0.08
68 F_2						
Observed		48	16	64		
Theoretical(3:1)		48	16		0.00	1.00
71 F_2						
Observed		147	51	198		
Theoretical(3:1)		148.5	49.5		0.06	0.80
74 F_2						
Observed		92	29	121		
Theoretical(3:1)		90.75	30.25		0.07	0.79

TABLE X

Summary of the inheritance of yellow seedlings in cross (1 x 14).

Pedigree and ratio	True green	Di-hybrid	Mono-hybrid	Total segr.	Total green
63					
F_2, Observed					102.0
Theoretical corrected*					102.2
F_2 families					
Observed	36.0	24.0	12.0	36.0	
Theoretical corrected*	36.0	18.8	17.1		
F_3, Observed					2726.0
Theoretical corrected*					2721.8
F_3 from dihybrid F_2					
Observed					864.0
Theoretical corrected*					866.0
F_3 from monohybrid F_2					
Observed					337.0
Theoretical corrected*					330.7
F_3 families					
Observed	770.0			174.0	
Theoretical corrected*	729.0			216.0	
F_4, Observed					29,831.0
Theoretical corrected*					29,314.0
F_4 families from selected monohybrid F_3					
Observed	44.0		73.0		
Theoretical (1:2)	39.0		78.0		
corrected*	44.0		73.0		
F_5 from selected F_4					
Observed					2,290.0
Theoretical (3:1)					2,040.0
corrected*					2,277.6

*See text.

TABLE X

inheritance of yellow seedlings
n cross (1 x 14).

	True green	Di-hybrid	Mono-hybrid	Total segr.	Total green	Yellow	N	X^2	P
					102.0	4.0	106		
ed*					102.2	3.8		0.01	0.92
	36.0	24.0	12.0	36.0			72		
ed*	36.0	18.8	17.1					2.93	0.24
					2726.0	92.0	2,818		
ed*					2721.8	96.2		0.19	0.65
					864.0	34.0	898		
ed*					866.0	32.0		0.13	0.71
					337.0	58.0	395		
ed*					330.7	64.3		0.73	0.40
	770.0			174.0			944		
ed*	728.0			216.0				10.58	0.002
					29,831.0	635.0	30,466		
ted*					29,314.0	1,152.0		241.00	0.000
ted									
	44.0		73.0				117		
	39.0		78.0					0.96	0.32
ed*	44.0		73.0					0.00	0.99+
					2,290.0	430.0	2,720		
					2,040.0	680.0		122.54	0.00
ed*					2,277.6	442.4		0.42	0.53

TABLE XI

Summary of the inheritance of Valencia plant type from the F_3 generation of cross (1 x 14)

	Breeding behavior of F_3 plants				N	X^2	P
	All non-valencia	15:1	3:1	All Valencia			
Observed	47.0	5	16	4.0			
Theoretical*	39.5	10	18	4.5	72	4.03	0.25
	Summary of F_3 families breeding 15:1						
	Non-valencia			Valencia			
Observed	92.0			7.0	99		
Theoretical*	88.1			10.9		1.57	0.21
	Summary of F_3 families breeding 3:1						
	Non-valencia			Valencia			
Observed	174.0			47.0	221		
Theoretical	165.8			53.2		1.64	0.20

*Corrected for small numbers - see text.

TABLE XII

Values of F* in tests for regression of various characters on rest period in cross (1 x 14), with rest period classified in groups by three different methods as indicated

Dependent variables		F3 rest period by Equal interval		Equal frequency		Indep families Norm
		Between**	Within**	Between	Within	Between
Rest period	F_3					
	F_4	37.73		11.99		22.60
Percent yellow $l_1l_1l_2l_2$	F_3				1.65	
	F_4				1.65	
Seed length	F_2				1.65	
	F_3				1.35	
Seed shape	F_2				1.75	
Seed coat color	F_2				2.55	
Indented seed	F_2			2.25		
	F_3			1.15		
Ruptured testa	F_2			1.10		
	F_3				1.15	
Black eyed seeds	F_3				1.10	
Fill of seeds	F_2		1.49		1.75	1.16
	F_3		3.53	2.00		1.92
Three-celled nuts	F_2			2.74		
	F_3				2.30	
Cells per nut	F_2				2.65	
	F_3				1.45	
Cells per plant	F_2	1.01		7.49		2.50
	F_3		2.39	3.00		
Fertility	F_3			1.20		
Pericarp thickness	F_2				7.35	
	F_3				1.75	
Pubescent pericarp	F_3			1.70		
Plant weight	F_2		1.05	4.16		3.4
Weight nuts	F_2		1.14	4.11		2.5
Valencia type	F_3				1.40	
Stipular spines	F_2	1.16			1.45	
	F_3		1.46		1.36	
Anthocyanin	F_2			1.90		
	F_3				2.25	
Length of season	F_2			1.61		
	F_3				1.10	
Angle of branches	F_2				1.85	
	F_3			1.41		
F_1 (P = 0.05)		2.16	3.35	2.16	3.35	2.1
F_1 (P = 0.01)		2.95	5.80	2.95	5.80	2.9

*Ratio of mean squares, Snedecor (1934).
**The headings, "Between" and "Within" indicate which was the larger mean square in the ratio, F.

Independent variable, dormancy								
by	families				F4 rest period by F2 families			
cy	Normalized		Equal interval		Equal frequency		Normalized	
hin	Between	Within	Between	Within	Between	Within	Between	Within
	22.60		90.47		6.00		20.29	
65					1.15			1.08
65					1.15			1.00
65						1.45		1.16
35						1.55		1.26
75					1.00			1.11
55						5.40		11.48
					1.15			1.94
						1.50	1.40	
					1.25		2.15	
15					1.30		2.41	
10						1.13		1.60
75	1.16		2.56		3.10			1.61
	1.92		13.40		1.18		1.44	
					1.80			2.72
30						3.10		1.32
65						1.25	1.33	
45					1.15		1.57	
	2.50		1.72		1.70		1.77	
		1.05		1.01	3.30			1.28
					1.13			2.74
35						1.90	1.30	
75						1.20	1.02	
						1.65		1.69
	3.46		1.56		1.85		1.88	
	2.54		2.62		2.65		1.90	
40						1.00		1.07
45		1.10	1.71		2.20			2.06
56		1.13	5.48		1.50		1.94	
					1.40		1.41	
35					1.55		1.03	
						1.10		1.19
10						1.10		2.77
35						1.60		1.70
						1.15		1.10
55	2.16	3.35	2.16	3.35	2.16	3.35	2.16	3.35
30	2.95	5.80	2.95	5.80	2.95	5.80	2.95	5.80

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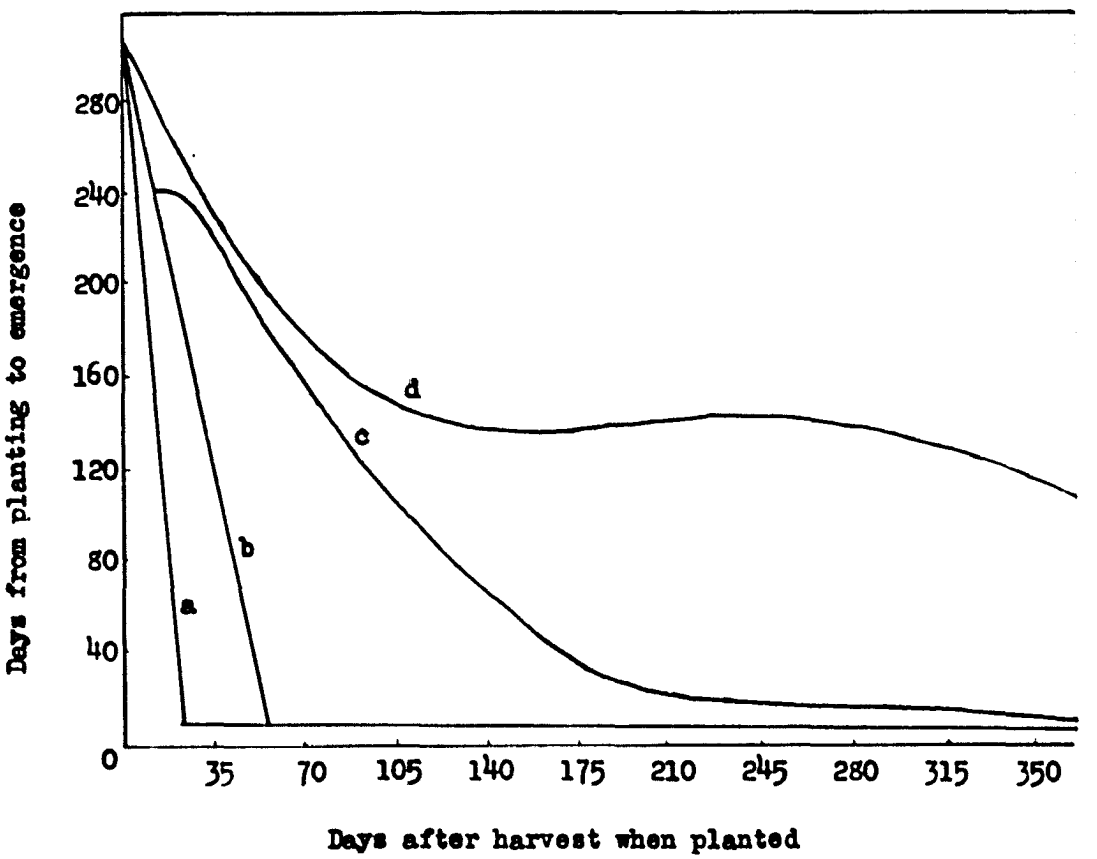

Figure 1.- Progress of after-ripening measured by time from planting to emergence in Florida Runner peanuts with different conditions of storage: (a) Storage in covered container at 40° C., continuously after harvest; (b) Shed storage at mean temperature of 20 - 25° C.; (c) Shed storage 12 days after harvest, then at 3° C.; (d) Storage at 3° C. continuously after harvest.

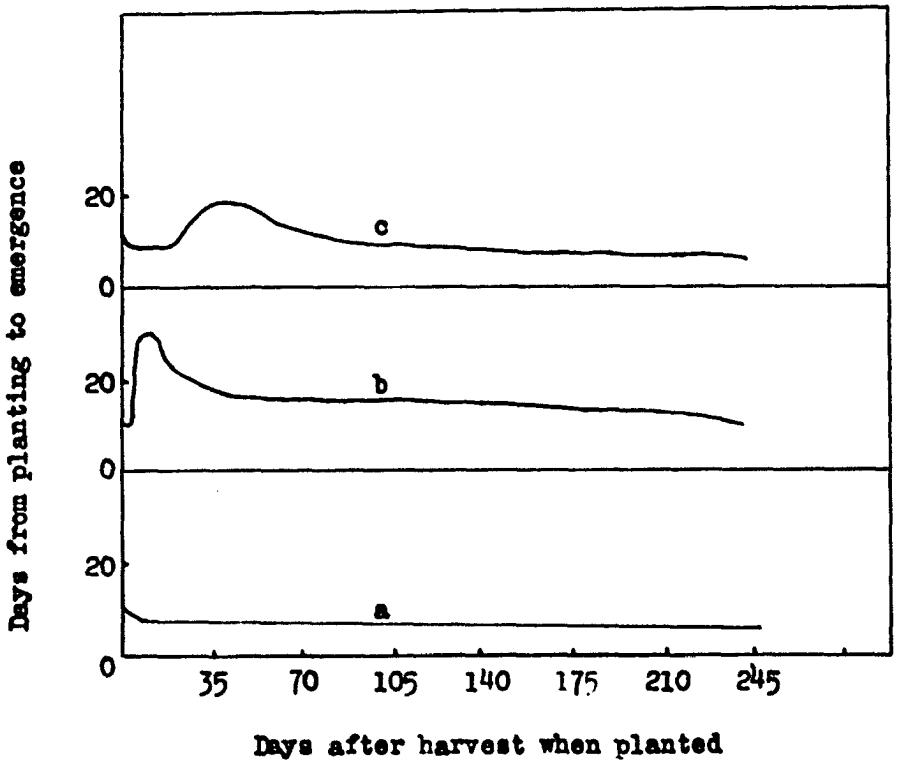

Figure 2.- Progress of after-ripening measured by time from planting to emergence in Spanish peanuts, Strain No.1, with different conditions of storage: (a) Shed storage at mean temperature of 20 - 25° C., continuously after harvest; (b) Shed storage 48 hours after harvest, then at 3° C.; (c) Shed storage ten days after harvest, then at 3° C.